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Transpiration responses to vapor pressure deficit in well watered 'slow-wilting' and commercial soybean

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Abstract

Slow-wilting has been observed in several soybean genotypes as a phenotypic response to drought stress. This trait has been proposed as useful in improving the yield of soybean under drought conditions, but the exact nature of the trait is unresolved. This research explored the hypothesis that slow-wilting is an expression of soil water conservation that results from a plant-imposed limitation on maximum transpiration rate. Therefore, gas exchange by slow-wilting and commercial genotypes was measured over a range of atmospheric vapor pressured deficit (VPD). Two experiments were undertaken to examine the response by whole plants and by plant canopies. The results showed that indeed the slow-wilting genotypes reached a maximum transpiration rate at a VPD of about 2.0 kPa with little or no further increase in transpiration rate above this value as VPD was increased. In contrast, the commercial cultivars showed continued increases in transpiration rate as VPD was increased above 2.0 kPa. These results indicated that the slow-wilting trait would be especially desirable in low humidity (high VPD) environments where water deficits commonly develop in the later part of the season. In these environments, restricted transpiration rate during the middle of the day with high vapor pressure deficit would result in water conservation allowing for both increased yield and water use efficiency.

Keywords: Slow-wilting; Soybean; Transpiration; Vapor pressure deficit

1. Introduction

Atmospheric evaporative demand, and consequently crop transpiration increase with increasing atmospheric vapor pressure deficit (VPD) (Sinclair and Bennett, 1998). Atmospheric VPD and transpiration rates follow a diurnal pattern, being lowest at sunrise and increasing to a maximum at around 15:00 (e.g. Hirasawa and Hsiao, 1999). However, the increase in transpiration has limits and a limiting maximum transpiration rate is commonly reached at a VPD of ~2.0 kPa (Turner et al., 1984; Comstock and Ehrleringer, 1993). Similarly, Bunce (1981) showed decreased stomatal conductance (limitation on transpiration) in a number of species, including soybean, between VPD of 1.0 and 2.5 kPa. Although these studies showed a similar pattern, the transpiration response differs both among (e.g. Turner et al., 1984) and within species (Salih et al., 1999; Isoda and Wang, 2002).

In soybean, Bunce (1984) demonstrated a lower stomatal conductance at an atmospheric VPD of 3.0 kPa compared with 1.0 kPa, and found genotypic differences in the response. Unfortunately, these tests only used a high and low VPD and did not examine the entire response to a range of VPD. Furthermore, only the leaf being measured was subjected to the VPD treatment and the transpiration response to VPD may be associated with whole plant hydraulics.

A limit on maximum transpiration rate could be particularly important in non-irrigated crop production. In a simulation analysis, Sinclair et al. (2005) demonstrated that imposition of limited maximum transpiration rates increased sorghum yields in 76–90% of seasons in a semi-arid environment. This outcome was due both to the water savings associated with reduced transpiration and to increased transpiration use efficiency (TUE). The systems analysis of Sinclair and Muchow (2001) showed that decreased radiation use efficiency (RUE) could increase maize yields in water-limited environments. However, when

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water was not limiting, the associated lower growth rate resulted in yield penalties (Sinclair and Muchow, 2001; Sinclair et al., 2005).

Crop photosynthesis is proportional to the transpiration rate multiplied by VPD divided by a transpiration efficiency coefficient (Tanner and Sinclair, 1983). A limited maximum transpiration rate that is reached when atmospheric VPD exceeds ~2.0 kPa would result in an afternoon depression of photosynthesis (e.g. Hirasawa and Hsiao, 1999; Pettigrew et al., 1990). The correlation in the decrease in corn and sorghum RUE with increasing VPD reported by Stockle and Kinry (1990) and Kiniry et al. (1998) is consistent with such a response. Limiting transpiration rate to a maximum would result in a restriction of evaporative cooling of leaves and concomitant increased leaf temperatures, which would be greatest when atmospheric VPD is greatest typically at about 15:00 (e.g. Isoda and Wang, 2002).

In non-irrigated soybean crops, water-deficit is a major yield-limiting factor and considerable effort has been spent identifying traits that will limit the yield reduction under drought (Purcell and Specht, 2004). In a drying soil the slow-wilting soybean genotypes PI 416937 (Hudak and Patterson, 1995; Sloane et al., 1990) and PI 471938 wilt 3–4 days later than commercial genotypes. However, the mechanism of this trait remains unresolved (Sinclair, 2004). These slow-wilting genotypes may have reduced transpiration rates compared with commercial genotypes resulting in significant soil water savings early in the season. For example, although the data of Sloane et al. (1990) were not statistically significant, under well-watered conditions leaf transpiration rates were 181 mg $H_2O\,m^{-2}\,s^{-1}$ for 'Forrest', and 168 mg $H_2O\,m^{-2}\,s^{-1}$ for PI 416937.

In this paper two experiments are presented to test the hypothesis that slow-wilting soybean genotypes have a maximum transpiration rate less than that of commercial genotypes. The first experiment measured transpiration in response to atmospheric VPD for individual plants of the two slow-wilting genotypes as compared to two commercial soybean genotypes. The second experiment examined diurnal photosynthesis and infra-red temperature data for complete canopies of one slow-wilting and one commercial soybean genotype in sunlit controlled-environment chambers.

Table 1
Sowing dates, measurement dates and dates of destructive leaf area and biomass harvests of the plants used in Experiment 1

	Block 1	Block 2	Block 3
Sowing	8 May	30 June	30 June
Measurement date	5 June (28) 7 June (30)	7 August (38)	10 August (41)
Destructive leaf area harvests	9 June (32)	9 August (40)	11 August (43)

The values in brackets are days after sowing.

2. Materials and methods

Both experiments were conducted at the University of Florida campus (29°38′N, 82°22′W) in Gainesville, FL. Experiment 1 was carried out in a glasshouse and Experiment 2 in Soil-Plant-Atmosphere Research chambers.

2.1. Experiment 1

Three blocks of soybean plants were used in Experiment 1. Each block consisted of the same four soybean genotypes (A5959 and Graham, both commercial genotypes; and PI 416937 and PI 471938, both slow-wilting genotypes) replicated three times. Thus each block contained twelve plants, which were organized in a completely randomized design. Sowing and measurement dates for each block are provided in Table 1.

The plants were sown into pots made from 100 mm diameter, 180 mm tall polyvinyl chloride pipes fitted with a flat end cap. The end cap had a small hole drilled in the centre for drainage. The top, open end of the pipes was fitted with toilet flanges for attaching the VPD chamber. Each pot was filled with Gardenplus top soil (#92432, Lowes Inc., North Wilkesboro, NC), inoculated with *Bradyrhizobium japonicum* (Nitragin, Brookfield, WI) and supplied with ~4 g of osmocote vegetable and bedding slow release plant fertilizer (14% N–6.1% P–10% K). Plants were watered every 2–3 days from sowing until measurements began.

To impose VPD treatments on the plants a small chamber system was attached to the pots at the time of measurement (Fig. 1).

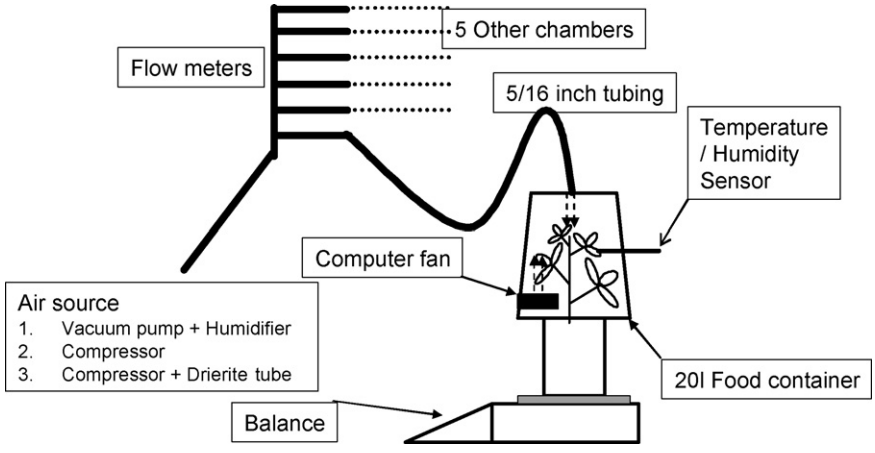

Fig. 1. Simple diagram of the system used to measure soybean transpiration responses to vapor pressure deficit. A full description is provided in the text.

The evening prior to measurements each pot was fully watered to dripping and a 340 mm diameter lid of a food container (Rubbermaid Commercial Products LLC, Winchester, VA) with the centre cut out was attached to the toilet flange at the top of the pot. Plants were sealed around the base using aluminum foil to eliminate soil evaporation into the chamber.

The following morning the aerial parts of the plants were sealed into a 21 L opaque plastic food container (Rubbermaid Commercial Products LLC, Winchester, VA) by placing the inverted container over the plant and sealing it into the previously installed lid. These containers extinguished approximately 25% of the solar radiation. The whole assembly was then placed in a shaded greenhouse. The light levels in the greenhouse were approximately 70% of irradiance incident to the greenhouse. Each container was equipped with a 12 V, 76 mm diameter computer box fan (Northern Tool and Equipment, Burnsville, MN) to mix the air inside the chamber. In addition, a pocket humidity/temperature pen (Extech Instruments, League City, TX) was mounted through the side wall of each container. Various humidity levels were achieved by flowing different air sources into these containers via plastic tubing (8 mm outside diameter) to balance the humidifying effect of the transpiring leaves. For each block of plants, three separate humidity levels were used. For each measurement the humidity was set and then the plant and air in the container were allowed to equilibrate for 10–15 min before measurements began. On each day, measurements were started at the highest humidity and then each of the mid humidity and low humidity settings were used in turn.

The configuration to achieve the highest humidity was different among blocks. In block 1 the highest humidity was achieved by flowing air at a low rate of 5 L min^{-1} into each chamber using two 57 L air compressors (Kobalt model L-215902, Lowe's Companies Inc., North Wilkesboro, NC). In blocks 2 and 3 the highest humidity was achieved by flowing air at 5 L min^{-1} using two pumps (DOA0P704, Gast, Benton Harbor, MI) with their intake tubes inside an atomizing humidifier (Herrmidifier, Sanford, NC). All flow rates were monitored using flow meters (Model FL-2043, Omega, Stamford, CT), one for each chamber.

The lower humidity treatments were obtained by changing the air flow rate into the plant chambers. In all blocks, mid humidity was achieved by flowing air into the containers at a rate of 25–30 L min^{-1} from the two compressors. The lowest humidity was achieved for all three blocks by flowing air from the two compressors through PVC tubes of 32 mm diameter filled with six-mesh indicating drierite (W.A. Hammond Drierite Co. Ltd., Xenia, OH) into the containers at a rate between 10 and 30 L min^{-1}. At each setting, the humidity levels varied greatly among chambers, even within a genotype, due to the size of individual plants. Therefore, in subsequent analyses the measured humidity in each chamber was used and no attempt was made to calculate a mean for the replicates of each block.

For each temperature and humidity setting the transpiration per plant was taken as the difference in mass between the start and end of each measurement. Mass was determined using portable balances (Model MXX-5, Denver Instrument, Denver, CO), which have a maximum capacity of 5000 g and a readability of 1 g. For each of the high and mid humidity treatments, transpiration rates were measured over a 20–35 min period. For the low humidity setting, transpiration rates were measured over a 10–20 min period. During each humidity treatment, air temperature and relative humidity were recorded two to three times. After each set of measurements plant leaf area was determined destructively by passing the leaves through an area meter (Model LI-3100, Licor, Lincoln, NE) on the dates indicated in Table 1. Whole plant transpiration rates were converted to transpiration per unit leaf area rates (T_r, mg H_2O m^{-2} s^{-1}).

Air temperature and relative humidity data were used to calculate the mean atmospheric VPD for each measurement. The data were analyzed by plotting T_r against VPD. There was a large amount of scatter among data points; therefore, the data for each genotype were grouped into cohorts of four consecutive values of VPD. The mean of both VPD and T_r for these cohorts were used in further analysis.

Two regression equations were applied to the grouped data using least-squares regression in Graph pad prism 2.01 (Graph pad Software Inc., San Diego, CA, 1996) for each genotype. Initially a double linear regression was applied to the data:

$$\text{If VPD} < X_0, \quad T_r = S_1(\text{VPD}) + C_1 \quad \text{(Line 1)}$$
$$\text{If VPD} \geq X_0, \quad T_r = S_2(\text{VPD}) + C_2 \quad \text{(Line 2)} \qquad (1)$$

where X_0 is the break point between the two line segments, S_1 and S_2 the slopes of the first and second line segments, respectively, and C_1 and C_2 are the constants of the first and second line segments, respectively. In the regression, the second line segment is constrained to intersect with the first line segment at X_0. The slopes of the two linear regressions (S_1 and S_2) were statistically compared to determine if they differed significantly ($p < 0.05$). If the slopes differed, the double-linear regression was retained. When the slopes were not significantly different, a simple linear regression was applied to all the data.

2.2. Experiment 2

Soil-Plant-Atmosphere Research chambers were used to measure gas exchange by entire canopies of different soybean genotypes when subjected to varying VPD. The controls and measurement capabilities of these chambers have been described in detail (Allen et al., 2003; Pickering et al., 1994). Briefly, the chambers have a soil surface area of 2 m^2 and soil depth of 0.6 m with the upper chamber having a height of 1.5 m. The sunlit chambers allow control of CO_2 concentration, and air and dew point temperatures. Measurements using a line quantum sensor (Model LI-191, Licor, Lincoln, NE) indicated that photosynthetically active radiation levels in the chambers were approximately 70% of those outside the chambers. Gas exchange data from the chambers were recorded and used to calculate and record whole canopy net carbon exchange rate (CER, μmol CO_2 m^{-2} s^{-1}) every 5 min. Canopy temperatures were also recorded using an industrial infra-red radiation thermometer (Omega Engineering, Stamford, CT) every 5 min. While the chamber system was designed to determine canopy transpiration rates, such data were not obtained because of difficulties with the equipment in measuring these data, and because of water condensation on the

chamber walls resulting from cool outside temperatures during the night. Canopy temperature measurements are presented as an indication of differences in transpiration rate. A comparatively high canopy temperature indicated a lower transpiration rate for that canopy.

Two soybean genotypes, PI 416937 (slow-wilting) and A5959 (commercial), were sown in these chambers on 19 December 2005. Three chambers of each genotype were sown in a completely randomized design. Seeds were sown in a square configuration at 150 mm spacing resulting in a plant population of 44 m^2. Two seeds were sown per space and the plants were subsequently thinned on 2 January 2006 (14 days after sowing). These plants were supplied with 120 g m^{-2} osmocote slow-release fertilizer, and were inoculated with *B. japonicum* (Nitragin, Brookfield, WI). The plants were watered daily to avoid water deficits. Initially plants were watered with overhead irrigation, but on 6 January a constant water table was established so that water did not limit CER or transpiration. Photoperiod was extended to ~15 h in order to maintain the canopies in a vegetative state. On 6 February, the photoperiod extension was ended and shade cloths were erected around the sides of each chamber at the height of the canopy to eliminate edge effects on CER measurements. The CO_2 within the chambers was maintained at 400 μL CO_2 L^{-1}.

Dew point temperatures were set constant at 14 °C and air temperatures were set to follow a harmonic change between a minimum of 22 °C at 07:00 EST and a maximum of 32 °C at 15:00 EST. Therefore, the atmospheric VPD in the chambers was set to vary from 1.0 to 3.2 kPa through the daily cycle. The chambers tracked these set values well except for a slight increase in midday dew point temperature to approximately 15 °C (Fig. 2). Therefore, maximum atmospheric VPD was slightly lower (~2.6–2.8 kPa) than the set value during the middle of the day (Fig. 2). There were no significant differences ($p < 0.01$) for either the air temperature or the dew point temperature experienced by the two genotypes. Therefore comparisons of canopy temperature were a valid indicator of canopy transpiration rates. These settings were maintained for both the growth and measurement phases.

Detailed measurements of CER and canopy temperature were recorded from 7 to 23 February. However, data from 13 February and 16 February were representative of the overall pattern and only results from these days are presented. Solar radiation interception was measured on 14 February by taking above canopy and below canopy readings with the line quantum sensor. All canopies intercepted 95% or more of the incoming solar radiation.

On 27 February, the middle three rows in each chamber were destructively harvested. The number of plants in each sample was recorded as was the total number of plants remaining in each chamber. The plants were clipped at the soil surface and these were separated into stem and leaf fractions. A sub-sample

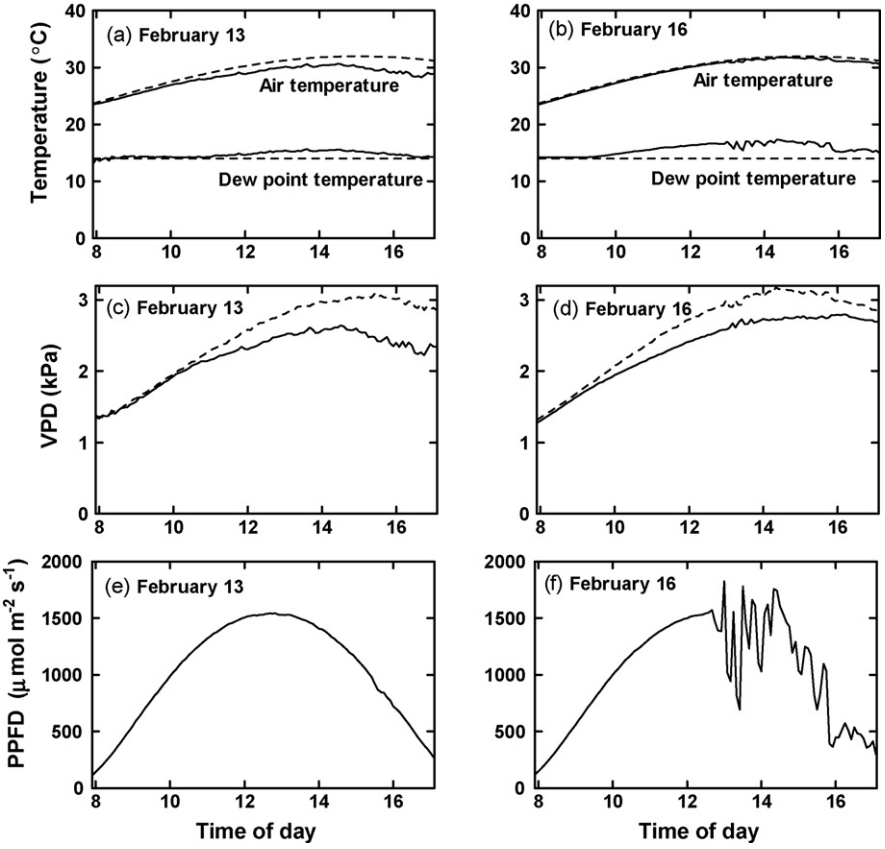

Fig. 2. Set (dotted lines) and obtained (solid lines), air and dew point temperatures (a and b), vapor pressure deficits (c and d) and photosynthetically active radiation (e and f) in the SPAR chambers on 13 and 16 February.

of ~2000 cm^2 was measured using a LI-3100 area meter. This leaf area sub-sample, the remaining leaves and the stem fraction were all dried in a fan forced oven to a constant weight. These values were then used to calculate leaf area index (LAI) for each Soil-Plant-Atmosphere Research chamber. At the end of the experiment, LAI was 6.9 for PI 416937 and 5.8 for A5959.

3. Results

3.1. Experiment 1

Air temperatures inside the humidity containers were normally distributed with a mean temperature of 34.9 ± 1.8 °C (S.D.). Relative humidity ranged between 37 and 82%. Calculated VPD were between 1.1 and 3.7 kPa for all humidity settings and soybean genotypes.

For three of the genotypes tested, A5959, Graham and PI471938, T_r response to increasing VPD was found to be linear ($R^2 \geq 0.70$) over the whole range of tested VPD. The slopes were 26.0 ± 4.8 (S.E.M.), 22.5 ± 3.6 and 21.0 ± 5.6 mg H_2O m^{-2} s^{-1} for each 1 kPa increase in VPD, respectively (Fig. 3). In contrast, the response of T_r to VPD of PI416397 was fitted best by the original double-linear response ($R^2 = 0.97$). At low VPD, T_r for this genotype increased by 30.8 ± 3.0 mg H_2O m^{-2} s^{-1} for each 1 kPa increase in atmospheric VPD up to an X_0 of 2.13 ± 0.07 kPa, above which there was no further increase in T_r between a VPD of 2.13 and 2.90 kPa (Fig. 3). The plateau value of T_r in this genotype was approximately 42 mg H_2O m^{-2} s^{-1}.

Extrapolation of S in A5959 and S_1 in PI 416937 to zero T_r indicated that the intercept would occur at an atmospheric VPD greater than zero. This result appears likely to be a consequence of calculating atmospheric VPD rather than a VPD based on leaf temperature, which was cooler than air temperature resulting in a lower saturated vapor pressure.

3.2. Experiment 2

Both A5959 and PI 416937 showed a similar diurnal change in CER. Only 2 days of data from nearly cloudless days are presented in Fig. 4, but all days showed a similar pattern. Initially CER was low early in the morning and then increased as the solar radiation increased. However, at approximately 10:00 the CER of the two genotypes began to differ on all days. The CER in the period from 10:00 and 15:00 was between 4 and 6 μmol m^{-2} s^{-1} greater in A5959 than in PI 416937 canopies on 13 and 16 February (Fig. 4).

Plots of canopy temperature showed that PI 416937 leaves were consistently warmer than A5959 leaves. The canopy temperature difference between genotype was approximately 1.5 °C at 08:00 and increased with atmospheric VPD and solar radiation to a maximum of approximately 3.0 °C around 15:00.

4. Discussion

The results of the two experiments demonstrated differences among soybean genotypes in their response of transpiration to atmospheric VPD. In Experiment 1 the slow-wilting genotype PI 416937 exhibited a clear limit on transpiration rate when VPD was greater than 2.1 kPa (Fig. 3c). In contrast the commercial cultivars A5959 and Graham had continued increases in T_r above 2.1 kPa VPD of 26.0 and 22.5 mg H_2O m^{-2} s^{-1} kPa^{-1}, respectively (Fig. 3a and b). These results are consistent with the results in Experiment 2 in which CER during the middle of the day when VPD was high (Fig. 4a and b) was ~5 μmol CO_2 m^{-2} s^{-1} higher in A5959 as compared with PI 416937. The 3 °C higher canopy temperature in PI 416937 compared with A5959 is further evidence of a lower midday transpiration rate in this slow-wilting soybean genotype (Fig. 4c and d).

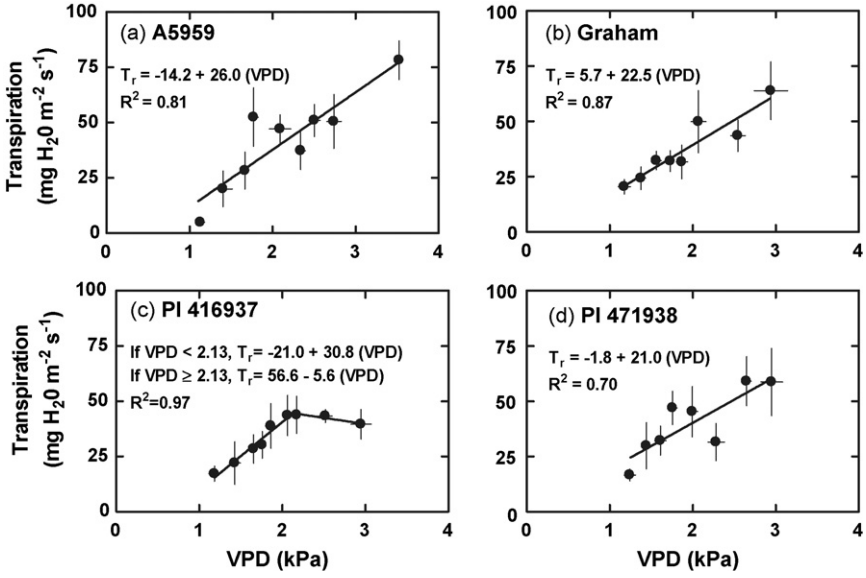

Fig. 3. Leaf transpiration rates of four soybean genotypes in response to VPD. Data are the mean of four consecutive data points and the error bars represent ± 1 standard error of the mean. Where no error bars are visible the error bars are smaller than the data points. The regressions in (a), (b), and (d) are single linear relationships and the regression in (c) is a double-linear relationship.

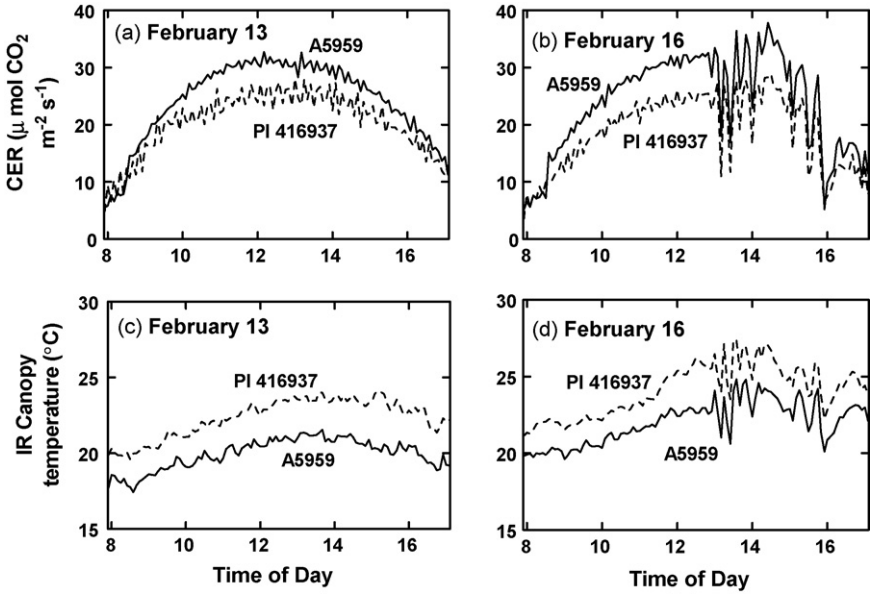

Fig. 4. Net carbon exchange rates (CER) on 13 February (a) and 16 February (b); and canopy IR temperatures for the canopies on 13 February (c) and 16 February (d) of PI 416937 and A5959 soybean canopies grown in SPAR chambers in Gainesville, FL. Data are the mean of three chambers.

A limitation on maximum transpiration rates could be a key trait in less humid regions where VPD is high and irrigation is not available by allowing a significant water saving (Sinclair et al., 2005) early in the season. Early season conservation of water would give the crop a soil water reserve to complete development and growth during seed fill. In addition, increasing the relative amount of water transpired in the morning when VPD is lowest compared with the afternoon, a limiting maximum transpiration rate will lead to small but important increases in crop TUE (Sinclair et al., 2005). Consequently, the limited soil water available for transpiration would allow the production of greater yield.

The water savings associated with maximum transpiration rates will be especially important in soybean where N_2 fixation rates are as high as 4.5 kg N ha^{-1} day^{-1} (Guafa et al., 1993) and are especially sensitive to water deficits (Sinclair et al., 1987). The decline in fixation is rapid when the fraction of transpirable soil water (FTSW) is less than ~0.5 (Sinclair, 1986). Therefore, every day that FTSW remains above 0.5 increases crop yield. Furthermore, this yield improvement will be greater where FTSW is less than 0.5 for a substantial time, due to intermittent rainfall.

However, a limiting maximum transpiration trait can have drawbacks. Where soil water supply is plentiful and there is no limitation to yield, a limiting maximum transpiration rate will result in decreased midday CER (Fig. 4) and may result in lower yields. For example, in a field scale test of 18 soybean genotypes with similar maturity, PI 416937 had the second lowest yield which was only 64% of the average yield (Cho et al., 2003). All genotypes tested were of similar maturity (MG IV-VI) and took 118 ± 4 days to maturity. Analysis of historical weather data from this location (http://www.wunderground.com/cgi-bin/findweather/getForecast?query=Carbondale+IL) showed that mean midday atmospheric VPD exceeded 2.5 kPa on 20% of the days, which would be sufficient to reach the maximum transpiration rate of PI 416937 (Fig. 3). The low yield of PI 416937 under these climatic conditions is consistent with a limiting maximum transpiration rate (Fig. 3) and decreased photosynthesis activity (Fig. 4).

Under certain non-irrigated conditions, where VPD is high, those genotypes having a limited maximum transpiration rate may yield more due to significant water savings. Therefore, this trait may be particularly useful for breeding soybean genotypes specifically targeted to environments with high VPD and low water supply. A whole crop simulation analysis, similar to that of Sinclair et al. (2005), could be used to target this trait to specific regions. Even in regions where this trait is well adapted, however, it is likely that in some rainy seasons a limiting maximum transpiration rate will result in yield penalties. Consequently, a limiting maximum transpiration rate is likely to increase yield stability, but, with the associated disadvantage of yield penalties in high-yield potential seasons.

References

Allen Jr., L.H., Pan, D., Boote, K.J., Pickering, N.B., Jones, J.W., 2003. Carbon dioxide and temperature effects on evapotranspiration and water use efficiency of soybean. Agron. J. 95, 1071–1080.

Bunce, J.A., 1981. Comparative responses of leaf conductance to humidity in single attached leaves. J. Exp. Bot. 32, 629–634.

Bunce, J.A., 1984. Identifying soybean lines differing in gas exchange sensitivity to humidity. Ann. Appl. Biol. 105, 313–318.

Cho, Y., Njiti, V.N., Chen, Y., Lightfoot, D.A., Wood, A.J., 2003. Trigonelline concentration in field-grown soybean in response to irrigation. Biol. Plant. 46, 405–410.

Comstock, J., Ehrleringer, J., 1993. Stomatal response to humidity in common bean (*Phaseolus vulgaris*): implications for maximum transpiration rate, water-use efficiency and productivity. Aust. J. Plant Physiol. 20, 669–691.

Guafa, W., Peoples, M.B., Herridge, D.F., Rerkasem, B., 1993. Nitrogen fixation, growth and yield of soybean grown under saturated

soil culture and conventional irrigation. Field Crop Res. 32, 257–258.

Hirasawa, T., Hsiao, T.C., 1999. Some characteristics of reduced leaf photosynthesis at midday in maize growing in the field. Field Crop Res. 62, 53–62.

Hudak, C.M., Patterson, R.P., 1995. Vegetative growth analysis of a drought-resistant soybean plant introduction. Crop Sci. 35, 464–471.

Isoda, A., Wang, P., 2002. Leaf temperature and transpiration of field grown cotton and soybean under arid and humid conditions. Plant Prod. Sci. 5, 224–228.

Kiniry, J.R., Landivar, J.A., Witt, M., Gerik, T.J., Cavero, J., Wade, L.J., 1998. Radiation-use efficiency response to vapor pressure deficit for maize and sorghum. Field Crop Res. 56, 265–270.

Pettigrew, W.T., Hesketh, J.D., Peters, D.B., Woolley, J.T., 1990. A vapor pressure deficit effect on crop canopy photosynthesis. Photosyn. Res. 24, 27–34.

Pickering, N.B., Allen Jr., L.H., Albrecht, S.R., Jones, P., Jones, J.W., Baker, J.T., 1994. Environmental plant chambers: control and measurement using CR-10T dataloggers. In: Watson, D.G., Zazueta, F.S. (Eds.), Computers in Agriculture. Am. Soc. Agric. Eng., St Joseph, MI, pp. 29–35.

Purcell, L.C., Specht, J.E., 2004. Physiological traits for ameliorating drought stress. In: Boerma, H.R., Specht, J.E. (Eds.), Soybeans: Improvements, Production and Uses. Agronomy Monograph No. 16 (3rd ed.). Am. Soc. Agron., Crop Sci. Soc. Am., Soil Sci. Soc. Am., Madison WI, pp. 569–520.

Salih, A.A., Ali, I.A., Lux, A., Luxova, M., Cohen, Y., Sugimoto, Y., Inanaga, S., 1999. Rooting, water uptake, and xylem structure adaptation to drought of two sorghum cultivars. Crop Sci. 39, 168–173.

Sinclair, T.R., 1986. Water and nitrogen limitations in soybean grain production. 1. Model Dev. Field Crop Res. 15, 125–141.

Sinclair, T.R., 2004. Physiological traits for ameliorating drought stress. In: Proceedings of the VII World Soybean Research Conference, Foz do Iguassu, PR, Brazil, pp. 245–252.

Sinclair, T.R., Bennett, J.M., 1998. Water. In: Sinclair, T.R., Gardner, F.P. (Eds.), Principles of Ecology in Plant Production. CAB International, pp. 103–120.

Sinclair, T.R., Muchow, R.C., 2001. System analysis of plant traits to increase grain yield on limited water supplies. Agron. J. 93, 263–270.

Sinclair, T.R., Muchow, R.C., Bennett, J.M., Hammond, L.C., 1987. Relative sensitivity of nitrogen and biomass accumulation of drought in field-grown soybean. Agron. J. 79, 986–991.

Sinclair, T.R., Hammer, G.L., van Oosterom, E.J., 2005. Potential yield and water-use efficiency benefits in sorghum from limited maximum transpiration rate. Funct. Plant Biol. 32, 945–952.

Sloane, R.J., Patterson, R.P., Carter, T.E., 1990. Field drought tolerance of a soybean plant introduction. Crop Sci. 30, 118–123.

Stockle, C.O., Kinry, J.R., 1990. Variability in radiation-use efficiency associated with vapor pressure deficit. Field Crop Res. 21, 171–181.

Tanner, C.B., Sinclair, T.R., 1983. Efficient water use in crop production research or re-search? In: Taylor, H.M., Jordan, W.R., Sinclair, T.R. (Eds.), Limitations to Efficient Water Use in Crop Production. Am. Soc. Agron., Madison, WI, pp. 1–27.

Turner, N.C., Schulze, E.D., Gollan, T., 1984. The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. I. Species comparisons at high soil water contents. Oecologia 63, 338–342.